## Neutral Theory and Relative Species Abundance in Ecology

Igor Volkov<sup>1</sup>, Jayanth R. Banavar<sup>1</sup>, Stephen P. Hubbell<sup>2</sup> and Amos Maritan<sup>3</sup>

- 1 Department of Physics, 104 Davey Laboratory, The Pennsylvania State University, University Park, Pennsylvania 16802 USA
- 2 Department of Plant Biology, The University of Georgia, Athens, GA 30602 USA and The Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama
- 3 International School for Advanced Studies (S.I.S.S.A.), Via Beirut 2/4, 34014 Trieste, INFM and The Abdus Salam International Center for Theoretical Physics, Trieste, Italy

The theory of island biogeography<sup>1</sup> asserts that an island or a local community approaches an equilibrium species richness as a result of the interplay between the immigration of species from the much larger metacommunity source area and local extinction of species on the island (local community). Hubbell<sup>2</sup> generalized this neutral theory to explore the expected steady-state distribution of relative species abundance (RSA) in the local community under restricted immigration. Here we present a theoretical framework for the unified neutral theory of biodiversity<sup>2</sup> and an analytical solution for the distribution of the RSA both in the metacommunity (Fisher's logseries) and in the local community, where there are fewer rare species. Rare species are more extinction-prone, and once they go locally extinct, they take longer to re-immigrate than do common species. Contrary to recent assertions<sup>3</sup>, we show that the analytical solution provides a better fit, with fewer free parameters, to the RSA distribution of tree species on Barro Colorado Island (BCI)<sup>4</sup> than the lognormal distribution<sup>5, 6</sup>.

The neutral theory in ecology<sup>2, 7</sup> seeks to capture the influence of speciation, extinction, dispersal, and ecological drift on the RSA under the assumption that all species are demographically alike on a per capita basis. This assumption, while only an approximation<sup>8, 9, 10</sup>, appears to provide a

useful description of an ecological community on some spatial and temporal scales<sup>2, 7</sup>. More significantly, it allows the development of a tractable null theory for testing hypotheses about community assembly rules. However, until now, there has been no analytical derivation of the expected equilibrium distribution of RSA in the local community, and fits to the theory have required simulations<sup>2</sup> with associated problems of convergence times, unspecified stopping rules, and precision<sup>3</sup>.

The dynamics of the population of a given species is governed by generalized birth and death events (including speciation, immigration and emigration). Let  $b_{n,k}$  and  $d_{n,k}$  represent the probabilities of birth and death, respectively, in the k-th species with n individuals with  $b_{-1,k} = d_{0,k} = 0$ . Let  $p_{n,k}(t)$  denote the probability that the k-th species contains n individuals at time t. In the simplest scenario, the time evolution of  $p_{n,k}(t)$  is regulated by the master equation<sup>11, 12, 13</sup>:

$$\frac{dp_{n,k}(t)}{dt} = p_{n+1,k}(t)d_{n+1,k} + p_{n-1,k}(t)b_{n-1,k} - p_{n,k}(t)(b_{n,k} + d_{n,k})$$
(1)

which leads to the steady-state or equilibrium solution, denoted by P:

$$P_{n,k} = P_{0,k} \prod_{i=0}^{n-1} \frac{b_{i,k}}{d_{i+1,k}},$$
(2)

for n > 0 and where  $P_{0,k}$  can be deduced from the normalization condition  $\sum_{n} P_{n,k} = 1$ . Note that there is no requirement of conservation of community size. One can show that the system is guaranteed to reach the stationary solution (2) in the infinite time limit<sup>14</sup>.

The frequency of species containing n individuals is given by

$$\phi_n = \sum_{k=1}^{S} I_k,\tag{3}$$

where S is the total number of species and the indicator  $I_k$  is a random variable which takes the value 1 with probability  $P_{n,k}$  and 0 with probability  $(1 - P_{n,k})$ . Thus the average number of species containing n individuals is given by

$$\langle \phi_n \rangle = \sum_{k=1}^{S} P_{n,k}. \tag{4}$$

The RSA relationship we seek to derive is the dependence of  $\langle \phi_n \rangle$  on n.

Let a community consist of species with  $b_{n,k} \equiv b_n$  and  $d_{n,k} \equiv d_n$  being independent of k (the species are assumed to be demographically identical).

From Eq.(4), it follows that  $\langle \phi_n \rangle$  is simply proportional to  $P_n$ , leading to

$$\langle \phi_n \rangle = SP_0 \prod_{i=0}^{n-1} \frac{b_i}{d_{i+1}}.$$
 (5)

We consider a metacommunity in which the probability d that an individual dies and the probability b that an individual gives birth to an offspring are independent of the population of the species to which it belongs (density independent case), i.e.  $b_n = bn$  and  $d_n = dn$  (n > 0). Speciation may be introduced by ascribing a non-zero probability of the appearance of an individual of a new species, i.e.  $b_0 = \nu \neq 0$ . Substituting the expressions into Eq.(5), one obtains the celebrated Fisher logseries<sup>15</sup>:

$$\langle \phi_n^M \rangle = S_M P_0 \frac{b_0 b_1 \dots b_{n-1}}{d_1 d_2 \dots d_n} = \theta \frac{x^n}{n}, \tag{6}$$

where M refers to the metacommunity, x = b/d and  $\theta = S_M P_0 \nu/b$  is the biodiversity parameter (also called Fisher's  $\alpha$ ). We follow the notation of Hubbell<sup>2</sup> in this paper. Note that x represents the ratio of effective per capita birth rate to the death rate arising from a variety of causes such as birth, death, immigration and emigration. Note that in the absence of speciation,  $b_0 = \nu = \theta = 0$ , and, in equilibrium, there are no individuals in

the metacommunity. When one introduces speciation, x has to be less than 1 to maintain a finite metacommunity size  $J_M = \sum_n n \langle \phi_n \rangle = \frac{\theta x}{1-x}$ .

We turn now to the case of a local community of size J undergoing births and deaths accompanied by a steady immigration of individuals from the surrounding metacommunity. When the local community is semi-isolated from the metacommunity, one may introduce an immigration rate m, which is the probability of immigration from the metacommunity to the local community. For constant m (independent of species), immigrants belonging to the more abundant species in the metacommunity will arrive in the local community more frequently than those of rarer species.

Our central result (see Box 1 for a derivation) is an analytic expression for the RSA of the local community:

$$\langle \phi_n \rangle = \theta \frac{J!}{n!(J-n)!} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \int_0^{\gamma} \frac{\Gamma(n+y)}{\Gamma(1+y)} \frac{\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)} \exp(-y\theta/\gamma) dy,$$
(7)

where  $\Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt$  which is equal to (z-1)! for integer z and  $\gamma = \frac{m(J-1)}{1-m}$ . As expected,  $\langle \phi_n \rangle$  is zero when n exceeds J. The computer calculations in Hubbell's book<sup>2</sup> as well as those more recently carried out by

McGill<sup>3</sup> were aimed at estimating  $\langle \phi_n \rangle$  by simulating the processes of birth, death and immigration.

One can evaluate the integral in Eq.(7) numerically for a given set of parameters: J,  $\theta$  and m. For large values of n, the integral can be evaluated very accurately and efficiently using the method of steepest descent<sup>16</sup>. Any given RSA data set contains information about the local community size, J, and the total number of species in the local community,  $S_L = \sum_{k=1}^{J} \langle \phi_k \rangle$ . Thus there is just one free fitting parameter at one's disposal.

McGill asserted<sup>3</sup> that the lognormal distribution is a more parsimonious null hypothesis than the neutral theory, a suggestion which is not borne out by our reanalysis of the BCI data. We focus only on the BCI data set because, as pointed out by McGill<sup>3</sup>, the North American Breeding Bird Survey data are not as exhaustively sampled as the BCI data set, resulting in fewer individuals and species in any given year in a given location. Furthermore, McGills analysis seems to rely on adding the bird counts of 5 years at the same sampling locations even though these data sets are not independent.

Figure 1 shows a Preston-like binning<sup>5</sup> of the BCI data<sup>4</sup> and the fit of our analytic expression with one free parameter (11 degrees of freedom) along with a lognormal having three free parameters (9 degrees of freedom). Stan-

dard chi-square analysis<sup>17</sup> yields values of  $\chi^2 = 3.20$  for the neutral theory and 3.89 for the lognormal. The probabilities of such good agreement arising by chance are 1.23% and 8.14% for the neutral theory and lognormal fits, respectively. Thus one obtains a better fit of the data with the analytical solution to the neutral theory to BCI than with the lognormal, even though there are two fewer free parameters. McGill's analysis<sup>3</sup> on the BCI data set was based on computer simulations in which there were difficulties in knowing when to stop the simulations, i.e. when equilibrium had been reached. It is unclear whether McGill averaged over an ensemble of runs, which is essential to obtain repeatable and reliable results from simulations of stochastic processes because of their inherent noisiness. However, simulations of the neutral theory are no longer necessary, and all problems with simulations are moot, because an analytical solution is now available.

The lognormal distribution is biologically less informative and mathematically less acceptable as a dynamical null hypothesis for the distribution of RSA than the neutral theory. The parameters of the neutral theory or RSA are directly interpretable in terms of birth and death rates, immigration rates, size of the metacommunity, and speciation rates. A dynamical model of a community cannot yield a lognormal distribution with finite variance

because in its time evolution, the variance increases through time without bound. However, as shown by Sugihara et al.<sup>18</sup>, the lognormal distribution can arise in static models, such as those based on niche hierarchy.

The steady-state deficit in the number of rare species compared to that expected under the logseries can also occur because rare species grow differentially faster than common species and therefore move up and out of the rarest abundance categories due to their rare species advantage<sup>19</sup>. Indeed, it is likely that several different models (e.g. an empirical lognormal distribution, niche hierarchy models<sup>18</sup> or the theory presented here) might provide comparable fits to the RSA data (we have found that the lognormal does slightly better than the neutral theory for the Pasoh data set<sup>20</sup>, a tropical tree community in Malaysia). Such fitting exercises in and of themselves, however, do not constitute an adequate test of the underlying theory. Neutral theory predicts that the degree of skewing of the RSA distribution ought to increase as the rate of immigration into the local community decreases. Dynamic data on rates of birth, death, dispersal and immigration are needed to evaluate the assumptions of neutral theory and determine the role played by niche differentiation in the assembly of ecological communities.

Our analysis should also apply to the field of population genetics in which

the mutation-extinction equilibrium of neutral allele frequencies at a given locus has been studied for several decades <sup>21, 22, 23, 24, 25, 26</sup>.

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Acknowledgements We are grateful to Oleg Kargaltsev for a careful reading of the manuscript. This work was supported by COFIN MURST 2001, NASA, by NSF IGERT grant DGE-9987589, by NSF grants DEB-0075102, DEB-0108380, DEB-0129874, and DEB-0206550 and by the Department of Plant Biology, University of Georgia.

Competing interests statement The authors declare that they has no competing financial interests.

Correspondence and requests for materials should be addressed to JRB (banavar@psu.edu) or to SPH (shubbell@dogwood.botany.uga.edu).

## Box 1

## Derivation of the RSA of the local community

We study the dynamics within a local community following the mathematical framework of McKane et al.<sup>27</sup>, who studied a mean-field stochastic model for species-rich assembled communities. In our context, the dynamical rules<sup>2</sup> governing the stochastic processes in the community are:

- 1) With probability 1-m, pick two individuals at random from the local community. If they belong to the same species, no action is taken. Otherwise, with equal probability, replace one of the individuals with the offspring of the other. In other words, the two individuals serve as candidates for death and parenthood.
- 2) With probability m, pick one individual at random from the local community. Replace it by a new individual chosen with a probability proportional to the abundance of its species in the metacommunity. This corresponds to the death of the chosen individual in the local community followed by the arrival of an immigrant from the metacommunity. Note that the sole mechanism for replenishing species in the local community is immigration from the metacommunity, which for the purposes of local community dynamics is treated as a permanent source pool of species, as in the theory of island

biogeography<sup>1</sup>.

These rules are encapsulated in the following expressions for effective birth and death rates for the k-th species:

$$b_{n,k} = (1-m)\frac{n}{J}\frac{J-n}{J-1} + m\frac{\mu_k}{J_M}\left(1-\frac{n}{J}\right),\tag{8}$$

$$d_{n,k} = (1 - m)\frac{n}{J}\frac{J - n}{J - 1} + m\left(1 - \frac{\mu_k}{J_M}\right)\frac{n}{J},\tag{9}$$

where  $\mu_k$  is the abundance of the k-th species in the metacommunity and  $J_M$  is the total population of the metacommunity.

The right hand side of Eq.(8) consists of two terms. The first corresponds to Rule (1) with a birth in the k-th species accompanied by a death elsewhere in the local community. The second term accounts for an increase of the population of the k-th species due to immigration from the metacommunity. The immigration is, of course, proportional to the relative abundance  $\mu_k/J_M$  of the k-th species in the metacommunity. Eq.(9) follows in a similar manner. Note that  $b_{n,k}$  and  $d_{n,k}$  not only depend on the species label k but also are no longer simply proportional to n.

Substituting Eq.(8) and Eq.(9) into Eq.(2), one obtains the expression<sup>27</sup>

$$P_{n,k} = \frac{J!}{n!(J-n)!} \frac{\Gamma(n+\lambda_k)}{\Gamma(\lambda_k)} \frac{\Gamma(\vartheta_k-n)}{\Gamma(\vartheta_k-J)} \frac{\Gamma(\lambda_k+\vartheta_k-J)}{\Gamma(\lambda_k+\vartheta_k)} \equiv F(\mu_k), \quad (10)$$

where

$$\lambda_k = \frac{m}{(1-m)} (J-1) \frac{\mu_k}{J_M}$$
 (11)

and

$$\vartheta_k = J + \frac{m}{(1-m)}(J-1)\left(1 - \frac{\mu_k}{J_M}\right). \tag{12}$$

Note that the k dependance in Eq.(10) enters only through  $\mu_k$ . On substituting Eq.(10) into Eq.(4), one obtains

$$\langle \phi_n \rangle = \sum_{k=1}^{S_M} F(\mu_k) = S_M \langle F(\mu_k) \rangle = S_M \int d\mu \widehat{\rho}(\mu) F(\mu).$$
 (13)

Here  $\hat{\rho}(\mu)d\mu$  is the probability distribution of the mean populations of the species in the metacommunity and has the form of the familiar Fisher logseries (in a singularity-free description<sup>15, 28</sup>)

$$\widehat{\rho}(\mu)d\mu = \frac{1}{\Gamma(\varepsilon)\delta^{\varepsilon}} \exp(-\mu/\delta)\mu^{\varepsilon-1}d\mu, \tag{14}$$

where  $\delta = \frac{x}{1-x}$ . Substituting Eq.(14) into the integral in Eq.(13), taking the limits  $S_M \to \infty$  and  $\varepsilon \to 0$  with  $\theta = S_M \varepsilon$  approaching a finite value<sup>15, 28</sup> and on defining  $y = \mu \frac{\gamma}{\delta \theta}$ , one obtains our central result Eq.(7).

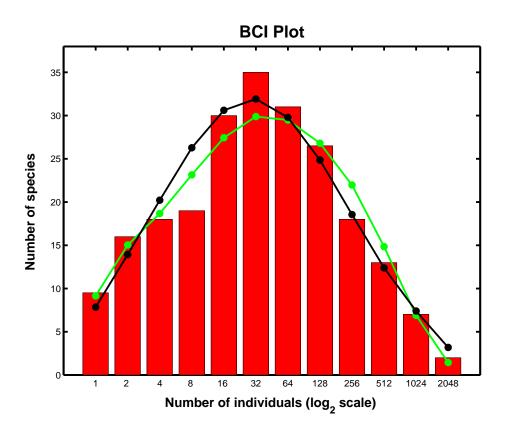


Figure 1: Data on tree species abundances in 50 hectare plot of tropical forest in Barro Colorado Island, Panama taken from Condit et al.<sup>4</sup>. The total number of trees in the dataset is 21457 and the number of distinct species is 225. The red bars are observed numbers of species binned into log(2) abundance categories, following Preston's method<sup>5</sup>. The first histogram bar represents  $\frac{\langle \phi_1 \rangle}{2}$ , the second bar  $\frac{\langle \phi_1 \rangle}{2} + \frac{\langle \phi_2 \rangle}{2}$ , the third bar  $\frac{\langle \phi_2 \rangle}{2} + \frac{\langle \phi_3 \rangle}{2} + \frac{\langle \phi_4 \rangle}{2}$ , the fourth bar  $\frac{\langle \phi_4 \rangle}{2} + \frac{\langle \phi_5 \rangle}{2} + \frac{\langle \phi_6 \rangle}{2} + \frac{\langle \phi_7 \rangle}{2} + \frac{\langle \phi_8 \rangle}{2}$  and so on. The black curve shows the best fit to a lognormal distribution  $\langle \phi_n \rangle = \frac{N}{n} \exp(-\frac{(\log_2 n - \log_2 n_0)^2}{2\sigma^2})$  (N = 46.29,  $n_0 = 20.82$  and  $\sigma = 2.98$ ), while the green curve is the best fit to our analytic expression Eq.(7) (m = 0.1 from which one obtains  $\theta = 47.226$  compared to the Hubbell<sup>2</sup> estimates of 0.1 and 50 respectively and McGill's best fits<sup>3</sup> of 0.079 and 48.5 respectively.)